THE

AMERICAN NATURALIST

Vol. XLIV April, 1910 No. 520

THE ORIGIN OF THE ELECTRICITY TISSUES IN FISHES[1]

PROFESSOR ULRIC DAHLGREN

Princeton University

Among the many specializations of animal tissues four are so fundamental in nature and so specific in their function that they stand out as exceptionally favorable objects for study, particularly as to their origin and evolution. These tissues are those which produce motion, heat, light and electricity in quantities, and for the benefit of the entire organism.

Of these, motion is the most important. Without the power to move it is probable that few animals would be able to survive and to evolve to any great degree of specialization. Thus the forms which did not develop organs of motion at an early period or those which lost it subsequently would be eliminated and would leave all other and higher degrees of specialization to be attained by such animals as had developed or retained muscle tissue.

Heat production was probably an important factor in the development of many land forms, especially in regions of the earth that became subject to cold, and the possession of any small part of this power would tell to a marked degree in the favorable selection of its possessor.

[1] Lecture delivered before the Society of American Naturalists in Boston on December 29, 1909. A fuller technical account with illustrations of the histogenesis of the electric tissue in *Gymnarchus* will shortly appear in another journal.

Of the other two abilities, that to produce light and to generate electricity, we find that both are rare. Luminosity is found to be widely distributed among the various kinds of animals, most of the principal groups having one or more representatives which can produce light. And yet this is, after all, a rare specialization and the percentage of animals which are luminous is very small indeed. It is not so absolutely necessary as the power to move nor can it be regarded as having the selective value that the possession of heat-producing tissues must have. Its real function, sexual, warning, or for purposes of seeing objects in the dark, has not been satisfactorily determined for any groups except possibly the deep-sea fishes and even here we find more to be without it than with it.

As to the last of the dynamic tissues, that which produces electricity, we have here a tissue which is remarkable to an extreme degree both for the rarity of its occurrence and its narrow distribution, is being confined to one group of vertebrates, the fishes, and found here among only seven families.

In these seven groups the tissue seems to have developed absolutely independently and to have formed seven separate types of organ differing markedly from one another in details of structure and position of the organ and yet all adapted, through certain analogous developments, to perform the same function.

We evidently have here a tissue of comparatively recent origin, phylogenetically, and one of the first studies to be made toward a knowledge of its evolution is to find out what can be learned from its history in the individual or its histogenesis.

Of the seven types of organs two are found in elasmobranchs and the remaining five in teleost fishes. The histogenesis of the two elasmobranch forms has been worked out by Ewart, Engelmann, Babuchin, Ogneff and others, but the corresponding history of this tissue in the teleosts has remained unproved with the exception of one form, *Gymnarchus,* the ontogenetic origin of whose electric organ the writer presents below.

Before explaining the histogenesis of the electric tissue in this teleost fish a brief résumé of what is known of the development of the two elasmobranch types of electric tissue should be given.

In the young embryos of *Raja*, Ewart and Engelmann found that the position of the future electric organ was occupied by well-developed muscle in no way different from the other muscle tissue of the trunk. In the half-developed fish the transformation of certain of these single muscle fibers into single electroplaxes was observed to begin, at a later period in those skates which had the simpler types of tissue, at an earlier time in those which had the more highly developed types. This change in the muscle fiber consisted of a widening of its anterior end, which finally resulted in the formation of a flat plate lying at right angles to the position of the former muscle fiber. The posterior end of the fiber degenerated, forming in some cases a useless tail-like appendage in other cases atrophying altogether.

During this change the myo-fibril bundles assumed various curved positions and formed the thick " striated " layer of the electroplax, while the larger part of the cytoplasm formed a flat anterior layer or "electric layer" as well as a thick covering, the nutritive layer, on the posterior surface. This posterior layer was produced into more or less developed papillæ. The nuclei multiplied by amitotic division and were segregated into the anterior and posterior layers, those in the anterior or electric layer forming a very regular layer themselves. The nerve supply, consisting of several medullated fibers, approached the anterior or electric surface and, dividing into very many fine naked branches, terminated in as many disc-shaped plates in this surface.

In the torpedoes, or electric rays, Ogneff has worked out the histogenesis and found that, as in the other elasmobranch forms (the skates), each electroplax develops from one muscle cell. But there are several important differences. The adult organ is a far more highly specialized structure in *Torpedo* than in *Raja* and the muscle cell is

still in a very young stage, a mere myo-blast possessing but one nucleus, at the time it begins to change. It is the end furthest from the electric surface or negative pole of the future electroplax that begins to enlarge first into a club-shaped form and then into a disc which continues to expand laterally and grow thinner until it becomes an exceedingly thin plate. The nucleus of the young myoblast or electroblast divides by amitosis into many nuclei, which are distributed through the plate and the nerve supply is large and ends in tiny discs that cover the whole upper, negative or "electric" surface.

In *Gymnarchus,* the only teleost whose histogenesis is known, the electroplaxes of the adult fish are arranged in eight long cylindrical masses, four on each side, and embedded in the muscle of the tail. Each cylinder consists of a row of the thick electroplaxes spaced apart by about their own length of the jelly-like "electric connective tissue" usually found in these organs. Each electroplax conforms to the outline of the cylinder laterally and is bounded anteriorly and posteriorly by surfaces from which a few short blunt papillæ emerge. The electroplax consists of a central core of a fibrillar nature, the fibrils being arranged in the form of approximate layers and giving the appearance of a transverse striation of this region. As will be seen below, this striation does not represent the striation of the voluntary muscle of vertebrates.

This core is covered by a layer of undifferentiated cytoplasm of moderate thickness which contains the numerous nuclei of the syncytium. The nuclei are arranged in a single layer, but, since the central core does not extend into the majority of the papillæ, the nuclei form a central mass in these appendages.

The nerve supply consists of several large medullated fibers which approach each electroplax from the rear and are easily seen to end on its posterior surface. Each of the naked ultimate branches terminates in a knobbed end plate which is imbedded in the substance of the outer

layer both on the papillæ and on the posterior surface itself.

The whole cylinder, both electroplaxes and electric connective tissue, is separated from the surrounding muscle tissue by a connective tissue sheath in which a few isolated pigment cells are to be seen. The electroplaxes do not exactly correspond in the adult either to the myotomes or to the vertebræ.

The significant development of the electric tissue takes place between the ninth day of embryonic life, at which time the embryo contains unchanged muscle tissue in its tail, and the 40-day embryo which possesses the organs in practically its adult condition. The critical changes take place within even closer limits; from the 11th day to the 15th would include them. The stages used in this examination were but four in number, the ninth, eleventh, twelfth and fortieth, four out of the seven valuable embryos given the writer by Dr. Arthur Shipley, Dr. Richard Assheton and Dr. J. Graham Kerr, to whom many thanks are due. This material was collected by Mr. John Samuel Budgett in Africa, he most unfortunately losing his life from fever shortly afterwards.

The ninth-day embryo shows no trace of any electric tissue. The myotomes, as shown in a longitudinal section are very regularly formed and are composed at this time of many perfect muscle fibers with the myofibrils developed in several bundles in the peripheral cytoplasm. These muscle fibers are all parallel with one another and with the long axis of the body. Connective tissue is but little developed although it is found sparingly between the muscle fibers.

In the embryo of eleven days the electric tissue has begun to form. Eight regions in each muscle segment, each region composed of a few (10–40) of the young muscle fibers, have become prominent through the slightly greater density of their cytoplasm and the beginning degeneration of the muscle cells which immediately surround them. These eight regions in each myotome lie directly in front of and behind eight corresponding

regions in the myotomes before and to the rear of them. They thus mark out anterio-posterior lines which represent the location of the future cylinders. The young muscle fibers composing them retain their myofibril bundles unchanged and the striation of these fibrils is exactly like that of all the other myofibrils in other muscle fibers. The multiplication of nuclei goes on by amitosis as in the regular muscle cells.

The next stages examined are seen in an embryo whose age was between twelve and fourteen days. The word "stages" is used because in such an embryo quite a range of developmental steps can be found, owing to the fact that the tail is still extending and consequently the anterior electroplaxes are older than the posterior. This condition is reversed in the adult, for here it can be seen that the posterior electroplaxes advance further in size and degree of specialization than the anterior ones did. A young stage in this embryo shows that the groups of cells in each myotome which are forming the electroplaxes have become so closely approximated that they form a larger syncytium composed of the several smaller syncytia or muscle fibers which went to form it. This mass has assumed a rather distinct, elongate, spindle-shaped form and each one has increased in length so as to overlap its neighbor both ahead and behind it by a third or more of its length. The myofibrils show a tendency to occupy the central core of the young electroplax and are still striated. In this stage the nerve supply can be seen approaching the spindle from somewhat behind its middle and coming in contact with it at about the junction of its middle and posterior thirds.

The older electroplaxes in this same stage show a change. This change consists in a segregation of the myofibrils in the central core of the mass, where they still run parallel with each other and in a straight anterior-posterior direction; except in the now swollen middle third of the structure where they have assumed a wave-like direction. Furthermore, they have lost the larger part of their striation, this feature being retained only in

either end of the fibrils. The less differentiated cytoplasm has become segregated into a peripheral layer and, owing to the more rapid growth in length of the entire body than of the individual electroplaxes, these latter have become drawn apart and no longer overlap as they did at an earlier date.

Before proceeding further a word is necessary as to the fate of the surrounding muscle fibers and the way in which the electroplaxes become marked off from the surrounding tissues.

At first the muscle cells that will be transformed into electric tissue are in direct contact with the surrounding muscle cells of the myotome. Then these immediately surrounding fibers begin to degenerate by a peculiar process of hystolysis that strangely enough resembles somewhat the formation of an electroplax. The middle of the fiber swells up and the myofibrils lose their striation; lastly the ends are drawn in, the nuclei fragment and the whole mass becomes a lump of amorphous matter that finally disappears.

The next developmental changes in the electroplax can perhaps be best described by comparing the stage last described with the practically adult electroplax. In this we find that the middle third of the young form has expanded into the cylindrical body of the completed stage. The two end portions have failed to grow in size and have become one of the several blunt papillæ that have evaginated from both ends. This comparative atrophy of the posterior end of the spindle has left the nerve ending on the posterior surface of the electroplax and on the evagination that project from it, while the anterior end is in contact with a considerable development of capillary blood channels that lie in the electric connective tissue.

Most interesting in this older stage is the fate of the myofibrils. They have lost their striation completely, the dark staining anisotropic substance seeming to have dissolved and left well-defined fibrils of the isotropic substance alone. These fibrils no longer lie so evenly together although still associated in groups. The wave-like

direction that they had previously assumed has increased until they now run back and forth at right angles to the axis of the electroplax and consequently in the same relation to their former course. This gives the striated appearance which might be taken for the degenerated remains of the real muscle striation that the developing electroplax formerly possessed.

We thus can see that, while the electroplax of *Raja* and of *Torpedo* were formed from single muscle cells, in the first case by a widening of the negative or electric end and in the second instance by a widening of the positive or nutritive end, the electroplax of *Gymnarchus* is formed by the association of several myoblasts into a single syncytium and the widening of the middle part of this structure into the electroplax.

The other anatomical features of *Gymnarchus* which have caused it to be classed with the *Mormyridæ* demand that a comparison of this organ be made with the apparently widely different organ found in the various mormyrus groups. That found in *Mormyrus Oxyrynchus* will serve as a type and its general plan has been well shown by Ogneff and Schlichter. Here it is evident that a number of consecutive and entire myotomes have been converted into electroplaxes and that the middle layer of each electroplax is composed of unaltered and clearly striated myofibril bundles. The large number of these fibril bundles and their distribution indicate that the whole electroplax is a syncytium composed of all or most of the cells which would otherwise have gone to make up the single myotome. In this we find an agreement with the electroplax of *Gymnarchus* which is also formed from several cells. In the one case all the cells in the myotome have been used; in the latter only those lying in eight particular localities.

Further homology is seen in the disposition of the probably superfluous myofibrils. In both forms they are relegated to a middle position in the electroplax while the apparently more important cytoplasm forms layers on the anterior and posterior surfaces of the structure. Also, in both, the now useless myofibril bundles are

packed out of the way at right angles to the axis of the electroplax which remains the same as the former axis of the muscle cells that were used to form it.

The only difference lies in the fact that the striation of the fibrils is retained in the *Mormyrus* forms while it is lost in *Gymnarchus,* the dark-staining anisotropic substance apparently dissolving away.

From what little can be predicted concerning the possible origin of the electric tissue in the other teleost forms it is probable that the Mormyridæ (including *Gymnarchus*) are the only fish in which the electroplax is formed as a syncytium from more than one cell. In *Astroscopus, Electrophorus* (forming *Gymnotus*) and *Malopterurus* the structures show every evidence of having been developed from single myoblasts with the exception of *Malopterurus,* where it is a question as to whether they are not evolved from gland cells instead.

The evolution of these structures was most probably not based upon a natural selective basis. It is true that all muscle cells produce a slight static discharge at the moment of contraction, and that the far greater shock given by the electroplax is possibly a development of this same discharge. But Darwin in his "Origin of Species" has already said that the electric organs of fishes were one of the serious obstacles in the way of his natural selection theory, showing that the very slight discharge of the more primitive organs could not possibly have been useful to their possessors to the extent of an excluding selection based on their presence or degree of development.

Some good evidence as to the methods of evolution ought to be deduced from the degree of specialization and distribution of electric organs in some of the groups; even if experimental work seems at present to be impossible. In the skates, for instance, we find a very even and general distribution of an organ and tissue that is apparently in course of evolution, but which has not yet arrived at a state of efficiency. It seems that the organ must have originated in the common ancestor of the thirty or more species of skates found in the seas of the world.

All the Rajidæ have this organ and yet their close allies show no sign of its appearance. One form in particular was formerly classed with the skates, but some years ago was removed on anatomical evidences from this group by D. S. Jordon and classed in another genus. The writer dissected a specimen of this species with great interest and care and found that there was no trace of electric tissue. And yet this species is undoubtedly closely related to the skates and must have inherited at least their potential powers to develop electric tissue. Furthermore this species is skate-like to an extreme degree in form and habit and must have lived under conditions and surroundings similar to those which we must assume were the ones, if any, that stimulated the skate ancestors to change muscle tissue into electric tissue. Evidently there are internal as well as external conditions and stimulæ to be taken into account.

Likewise among the torpedoes; all possess a very highly developed organ, evidently a common inheritance from some ancestor in which it originated. Subsequent variation in the tissue has not kept pace with the fair amount of external variation in the several species. It seems that the impulse to evolve this tissue has extended into all the members of these two groups, a real inner stimulus working independently of outer condition.

On the other hand, other groups of similar form, appearance and mode of life to some of the other electric fishes absolutely lack the electric tissues. These may or may not be nearly related. A rather remarkable example is to be seen in *Astroscopus* and its related form *Uranascopus scaber*. These two fish look so much alike that one may be used to show the fishermen what the other looks like. Their habits are practically the same. Also this feature is noticeable among the Gymnotidæ, whose various members show many grades of specialization but have not been sufficiently studied as to the possession of rudimentary electric organs. These studies together with the histogenesis of other teleost electric tissues, particularly that of *Malopterurus*, are most attractive fields for future work.